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Interspecific interactions between collembolan populations in culture

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With 4 figures

Synoposis: *Original scientific paper*

The effect on population growth of interspecific interactions was studied among 4 species of Collembola: *Folsomia candida* WILLEM, *Xenylla grisea* AXELSON, *Sinella caeca* (SCHÖTT) and *Pseudosinella violenta* FOLSOM under laboratory conditions. Interaction was examined mediated by three different mechanisms: direct interaction, substrate conditioning and airborne allomones. It was discovered that the results of the interaction between any two species usually varied greatly depending on the mechanism involved. In some cases one mechanism stimulated population growth while another inhibited it. Given the nature of Collembola habits and habitats it is likely that one mechanism will dominate under certain circumstances and another under different ones. The result is that it is impossible to categorize the interspecific interactions we observed by any of the standard terms for such interactions such as competition amensalism or cooperation.

Key words: competition, interspecific interaction; amensalism; Collembola; allomone; pheromone; substrate conditioning; population growth; airborne chemicals.

1. Introduction

Collembola are excellent organisms for laboratory study of interspecific interaction due to their small size (normal adult maximum size about 3 mm), and limited movement. Furthermore the many species which can be easily reared in captivity normally live in enclosed spaces which facilitate chemical and contact exchanges. Most species can reproduce on similar diets. Their short life spans (often less than a month from egg to egg) and ease of rearing make them excellent animals for laboratory studies. Their interspecific interactions are limited since none of these involve carnivory or parasitism (CHRISTIANSEN, 1964).

Earlier laboratory studies involving 11 species in 13 direct interactions (CHRISTIANSEN, 1967) showed that there were generally 3 types of results: (**1**) one species dominates from the start; (**2**) one species dominates initially but is eventually replaced by the second species; and (**3**) no dominance is displayed and the species seem capable of coexisting indefinitely. Varying temperature or light seldom had any significant impact on outcome. CULVER (1975) showed that in non-patchy cultures involving *Lepidocyrtus cinereus* FOLSOM and *Folsomia candida* WILLEM, *L. cinereus* won in about half of the trials and the two species were able to coexist in about half. When a patchy environment was furnished the result was coexistence in all cases. In direct contact interactions among *Sinella caeca* (SCHÖTT) *Hypogastrura (Ceratophysella) denticulata* (BAGNALL) and *Onychiurus armatus* (TULLBERG) (*sensu* STACH, 1954), *S. caeca* was generally the strongest and *armatus* the weakest reproducer (LONGSTAFF, 1976). Environmental conditions affected the outcome strikingly in one of the three interactions. LONGSTAFF also found that the starting numbers or ratios of animals could

affect results. VAN COTT (1982 unpublished thesis) studied interspecific interactions among *Entomobrya (Entomobryoides) guthriei* FOLSOM, *Cryptopygus thermophilus* (AXELSON), *Pseudosinella sexoculata* Schött, *Sinella curviseta* BROOK, and *Proisotoma schoetti* (DALLA TORRE). He found that *S. curviseta* was most successful and *C. thermophilus* least. He also reported that both interspecific and conspecific substrate conditioning had an impact on population growth.

The purpose of the present study was to extend our earlier work and to examine the effects of different conditions (direct interaction, substrate conditioning alone and airborne pheromones and allomones alone) involved in interspecific interactions in Collembola. We used 4 species belonging to 3 families. One of these species is usually parthenogenetic *(F. candida)* and the other three are bisexual.

There are 3 parts to this study involving: (**1**) direct interaction; (**2**) substrate conditioning; and (**3**) airborne factors. Direct interaction would involve mechanisms (**2**) & (**3**) but would add the dimension of individual contact. Techniques and protocols will be described first and then the reactions of different species pairs. In the final general discussion the overall picture created by these and other studies will be presented.

Since none of the interactions involve carnivory or parasitism (CHRISTIANSEN, 1964), most of the interactions we have studied might be called competition; however, this term is one which has many often contradictory definitions (KEDDY, 1989). We shall not attempt to define the nature of the interactions we examine here in terms of competition, amensalism or other terms usually used to describe interspecific interaction but merely call them interspecific interactions.

2. Methods and materials

2.1. Species studied

Four species were studied: *Folsomia candida*, *Sinella caeca*, *Xenllya grisea*, and *Pseudosinella violenta*). All possible interactions among the first three were examined, but available time limited experiments with the last to comparison with *F. candida*. These species afforded a wide taxonomic array (families Isotomidae, Entomobridae, Hypogastruridae and Entomobryidae respectively). They all reproduce well in culture chambers. They are all forms which almost certainly interact in their normal environments. In addition they were all species with similar egg to egg times and were relatively insensitive to environmental fluctuations (CHRISTIANSEN, 1967; LONGSTAFF, 1976).

All cultures were kept in total darkness under constant 20 °C temperature. Population counts were made every other week under laboratory light and temperatures and food and water was added. When numbers of animals became too great to count individually, a grid was placed on the chambers dividing the chambers into 8 or 16 sections. Animals were counted in one section and the process repeated 4 times. The total was estimated by multiplying this figure by 2 or 4. In all experiments the bottom of the container was covered to about 1 cm depth with a plaster of paris (9 parts)/charcoal (1 part) mixture. The charcoal fraction was 50% animal bone black, 50% activated (vegetable) charcoal. The chambers were aged for 3 days to avoid fresh chamber toxicity. The food used was baker's yeast and the cultures were kept moist with distilled water. Mold was removed when it occurred. Adult or subadult specimens were used as starting stocks in all experiments.

2.2. Direct interaction

These experiments used plastic dishes (11 cm diameter and 6 cm deep). An initial series of experiments was carried on for 18 weeks; however, these results indicated that the final outcome was clear by the end of 12 weeks. All subsequent experiments were carried out for 14 weeks. They were started with 10 specimens of each species except for *S. caeca* where 20 specimens were usually used to compensate for their low reproductive rate.

2.3. Substrate conditioning

All experiments were carried out in small plastic chambers 4.5 cm diameter × 4 cm deep. All studies save those involving *S. caeca* used 10 specimens for the initial seedings. Studies with *S. caeca* started

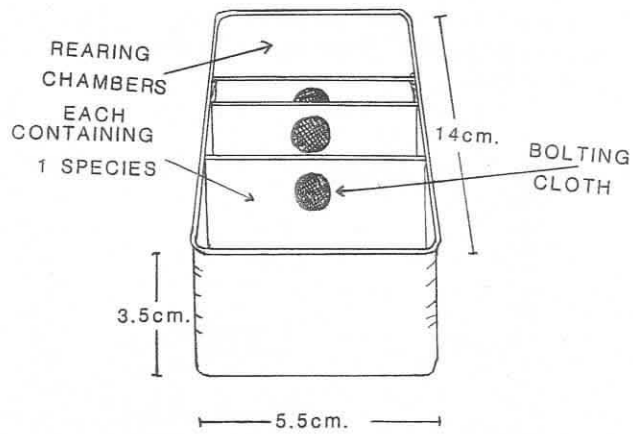

Fig. 1. Apparatus for airborne pheromone and allomone studies.

with 20 specimens. The conditioning species was allowed to stay in the chambers for 12 weeks. At the end of this time the specimens were removed and the chambers cleaned of fecal matter, exuviae and eggs. The chambers were then reseeded with 10 specimens either of the same species or 10 of the species to be tested for conditioning effects. The populations were initially allowed to grow for 14 weeks; however, it soon became clear that effects were noticeable earlier so the period was shortened to 12 weeks. This period encompasses the maximum growth phase of all species concerned (see CHRISTIANSEN, 1967 & LONGSTAFF, 1976). The growth rates of the populations in the unconditioned chambers were used as controls.

2.4. Airborne factors

A chamber was developed with 2 Vaseline covered lids and barriers separating the two populations under observation by a pair of 'cordon sanitaire' spaces allowing escapees to be recovered before they contaminated the opposite culture chamber (figure 1). In experimental chambers, these openings were covered by bolting cloth, allowing passage of gases between the chambers. Controls had impermeable barriers separating the two chambers. The experiments were run for either 12 or 14 weeks. Controls were compared both to allomonal and pheromonal chambers.

2.5. Statistical analysis

Most analyses of the results employed MINITAB. This is a statistical package available from Pennsylvania State University. In most experiments the last two counts for each culture were taken and a T test was run to obtain P values. In experiments where there was a lessening of difference between population sizes at the end of the experiment, the two counts where the populations were most different in numbers were used instead. In substrate conditioning comparisons between self conditioned chambers and unconditioned chambers (controls) we used only the 12 week counts since only this afforded comparable large numbers of individuals.

Outcomes of direct interaction were categorized in terms of types: (**1**) = one species dominates from start and eradicates other, (**2**) = one species dominates at start but was later replaced by second species, or (**3**) both species coexist indefinitely.

3. Results

3.1. *Folsomia candida vs. Xenylla grisea*

Direct interaction: *X. grisea* reproduced little or not at all when placed in direct interaction with *F. candida*. This agreed well with CHRISTIANSEN (1967). Breeding was stopped almost entirely in contrast to the controls (fig. 2A). *F. candida* population

growth was briefly stimulated by *X. grisea* (see figure 2B) but by week 8 the effect had disappeared. Thus the interaction of these species was of type 1 with *F. candida* the winner.

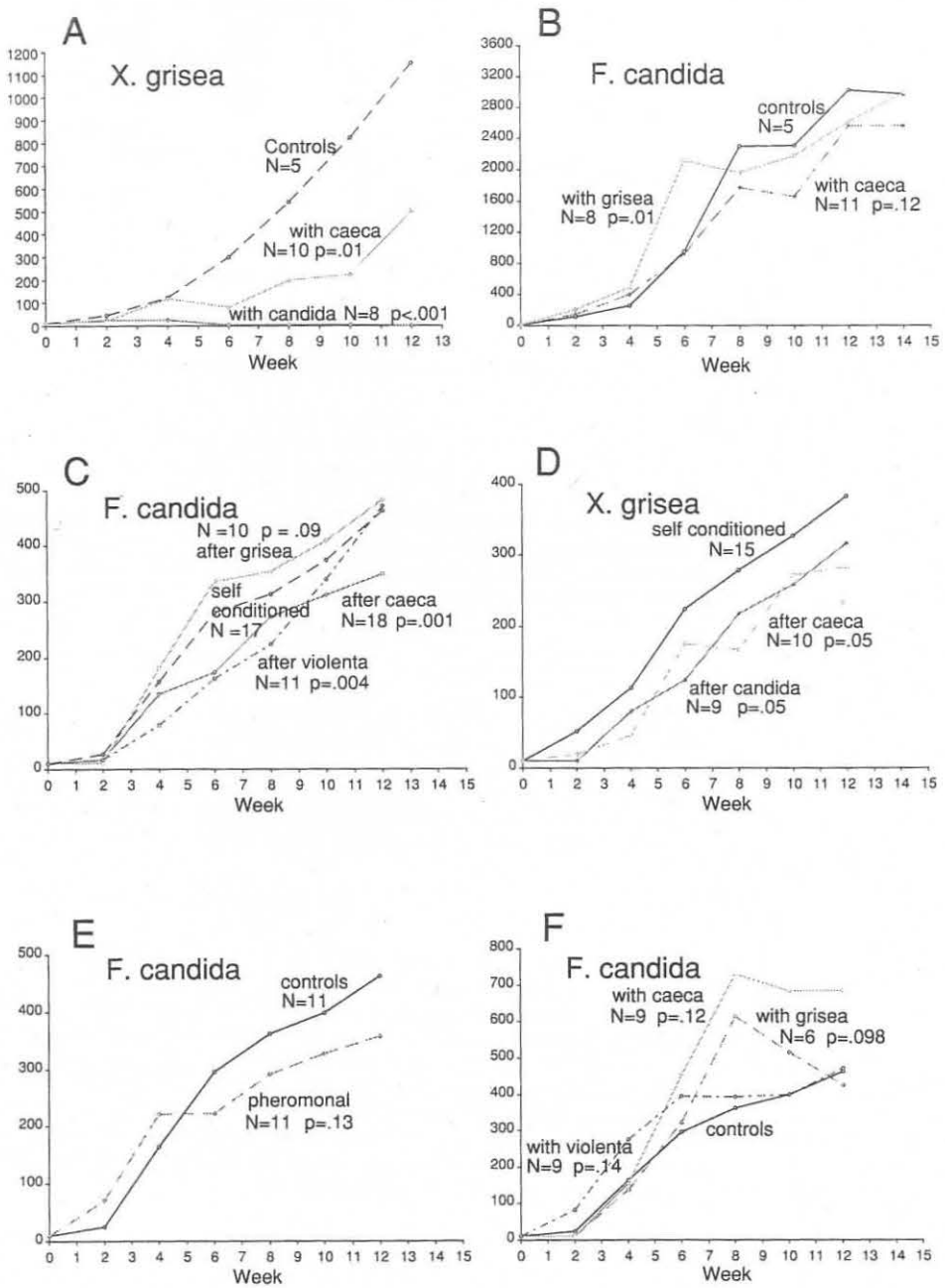

Fig. 2. Mean population growth of cultures under different conditions. N = numbers of replicates. p = probability that differences between the experimental condition and the control are not the result of random variation. (A) *Xenylla grisea* in direct interaction. (B) *Folsomia candida* in direct interaction. (C) *F. candida* in preconditioned chambers. (D) *X. grisea* in preconditioned chambers. (E) *F. candida* airborne pheromonal chambers. (F) *F. candida* airborne allomonal chambers.

Substrate conditioning: *X. grisea* had an apparent but not statistically significant stimulatory effect on *F. candida* (see figure 2C). On the other hand substrate conditioning by *F. candida* had a significant (P = .046) negative effect upon population growth in *X. grisea* (fig. 2D). Twelve week counts of unconditioned and self conditioned chambers of *F. candida* were very similar (means 305 and 290 respectively P = .61). The 6 week counts of *X. grisea* unconditioned chambers were higher than those in self-conditioned chambers (means 218 & 188) but the difference was not significant (P = .34).

Airborne factors: There appeared to be a pheromonal inhibition of population growth in *F. candida* (see figure 2E) but the difference was not significant (P = .13). *X. grisea* appeared to have had an inhibitory effect upon *F. candida* but it occurred only in the end and was not significant (see figure 2F). On the other hand *X. grisea* had a strong (p = .001) pheromonal inhibitory effect (see figure 3A) while *F. candida* had a strong (p = .0004) stimulatory effect (see figure 3B).

Overview: *F. candida* was not clearly affected by *X. grisea*, but population growth of the latter was strongly slowed or stopped by direct and/or substrate-mediated interaction with the former. In contrast population growth of *X. grisea* was strongly affected both positively and negatively by airborne chemicals.

3.2. *Folsomia candida vs. Sinella caeca*

Direct interaction: *S. caeca* had a slight but not significant (p = .12) inhibitory effect upon population growth of *F. candida* in direct interaction (fig. 2B). On the other hand, the latter had a strong inhibitory effect upon the former (fig. 3C).

Results of the direct interaction studies (type 1 with *F. candida* dominating from the start) were very surprising since our earlier studies CHRISTIANSEN, 1967) showed that at first *F. candida* dominated but shortly *S. caeca* increased and eventually dominated (type 2). Comparison of the original data of the two studies soon furnished one possible answer. Our stocks of *F. candida* used in the two experiments were different. The population growth rate of the 1985–89 stocks was almost twice as great as that of the 1967 stocks. In contrast the population growth rates of the two, again different, stocks of the sexual *S. caeca* were identical. These separate stocks may not explain the contrasting outcomes but it indicates a striking difference in vigor of the two *F. candida* stocks which makes the contradictory results not surprising. The stocks used in the present study were entirely parthenogenetic; however, those used in the 1967 study were at least partly bisexual. We recorded males from these populations but never found a male in the 1985–89 stocks.

Substrate conditioning: There was significant mutual inhibition in the case of substrate mediated factors (see figures 2C & 3D). The 6 week counts in *S. caeca* unconditioned chambers were higher than those in self conditioned chambers (means 18.7 & 14.4) but the difference was not significant (P = .40).

Airborne factors: *S. caeca* population growth appears to have been strongly depressed by airborne pheromones (see figure 3E); however, extreme variability among the experimental cultures (2 failed to reproduce) resulted in no statistical significance of the results (p = .34). Nevertheless a depressive effect was indicated. Population growth in *F. candida* appears to have been strongly stimulated by *S. caeca* (see figure 2F) but this was largely the result of one highly aberrant culture which had 3 times the normal population growth. When this culture was eliminated from calculation there was still a possible stimulatory effect but it was not significant (p = .12). Population growth in *S. caeca* appears to have been inhibited by airborne *F. candida* allomones but only after 8 weeks (see figure 3F) and then not strongly (p = .06).

Overview: *F. candida* had a generally negative influence upon population growth in *S. caeca* while *S. caeca* had mixed effects upon *F. candida*. Thus the outcome of interaction between these two species depended upon the nature of the interaction as well as the genetic makeup of the *F. candida* population.

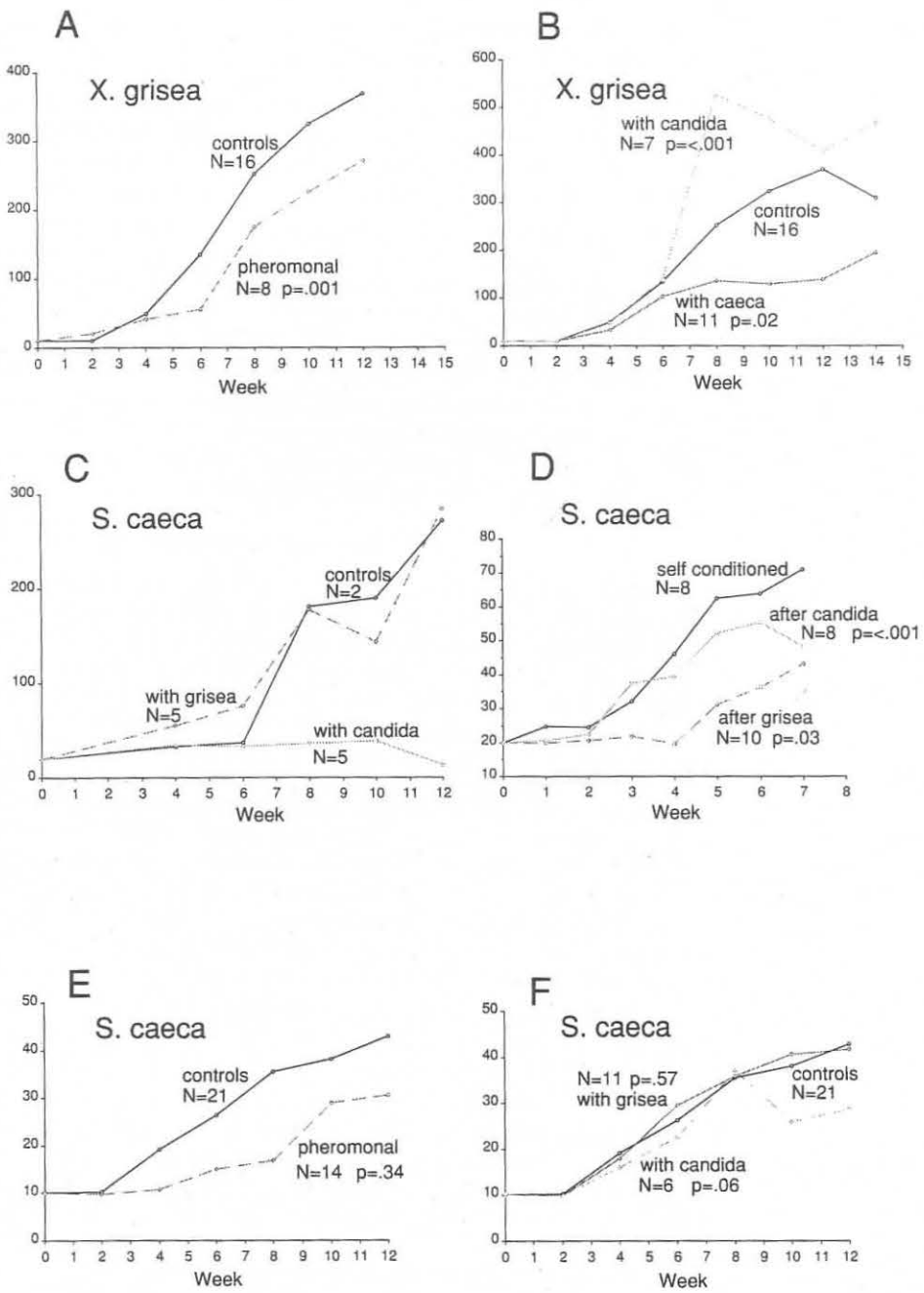

Fig. 3. As figure 2. (A) *X. grisea* airborne pheromonal chambers. (B) *X. grisea* airborne allomonal chambers. (C) *Sinella caeca* in direct interaction. (D) *S. caeca* in preconditioned chambers. (E) *S. caeca* airborne pheromonal chambers. (F) *S. caeca* airborne allomonal chambers.

3.3. *Sinella caeca vs. Xenylla grisea*

Direct interaction: population growth in *X. grisea* was strongly inhibited in direct interaction with *S. caeca* (fig. 2A); however, the interaction appears to be a type 3 in which

both species can persist indefinitely. Even at a reduced growth rate *X. grisea* reached far greater numbers than *S. caeca* whose growth rate was unaffected compared to controls (fig. 3C). Note that direct interaction with *S. caeca* involved two series of experiments which unfortunately could not be combined for statistical analysis, because of different seeding numbers. Those shown in fig. 3C were from one series but the other series had very similar results.

Substrate conditioning: there was mutual inhibition between *S. caeca* and *X. grisea* (see figures 2D & 3D). In both cases the inhibition was late in starting and at similar levels (p values .049 & .028).

Airborne factors: *S. caeca* was unaffected by airborne allomones produced by *X. grisea* (see figure 3F) while *X. grisea*'s growth was strongly (p = .019) inhibited by *S. caeca* (see figure 3B).

Overview: interactions between *S. caeca* and *X. grisea* were mixed with the final result strongly influenced by the nature of the interaction.

3.4. *Folsomia candida vs. Pseudosinella violenta*

Direct interaction: *P. violenta* had no significant effect upon *F. candida* population growth (p = .75) but population growth in *P. violenta* was statistically very significantly inhibited by F. candida (figs. 4A & 4B).

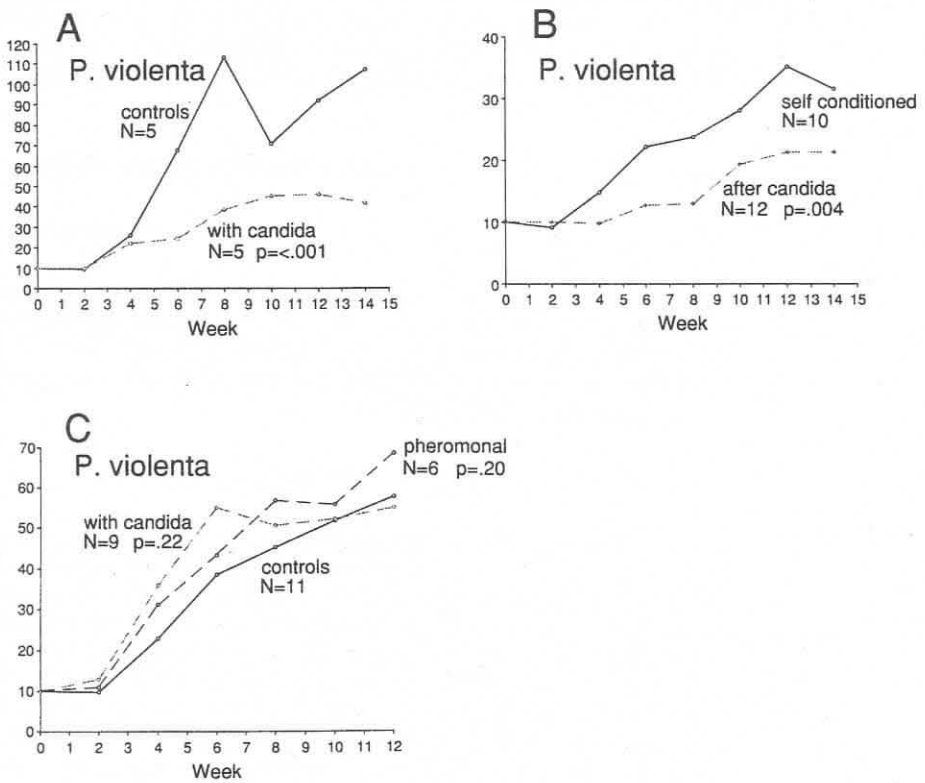

Fig. 4. As figure 2. (A) *Pseudosinella violenta* in direct interaction. (B) *P. violenta* in preconditioned chambers. (C) *P. violenta* in airborne pheromonal and allomonal chambers.

Substrate conditioning: population growth in *F. candida* was significantly (P = .0039) but temporarily slowed by conditioning by *P. violenta* (see figure 2C). Population growth in *P. violenta* was strongly slowed by conditioning by *F. candida* (fig. 4B). The 12 week counts in *violenta* unconditioned chambers were lower than those in self conditioned chambers (means 24.2 & 29.1) but the difference was not significant (P = .33).

Airborne factors: *F. candida* was not significantly affected by *P. violenta* (see figure 2F) but the latter species population growth was weakly but not significantly (p = .20 & .22) respectively stimulated both pheromonally and allomonally by *F. candida* (see figure 4C).

Overview: the interaction between *P. violenta* and *F. candida* was one where the former had no long term effect on the latter while the latter had mixed impact upon the former. The net result again would depend upon the nature of the interaction.

3.5. Number density dependence

We tested all substrate conditioning interactions for number density dependence. We compared the final numbers found in the test chambers with the final population sizes for the conditioning species before removal, using Spearman's rank order correlation. In no case was there a significant inverse correlation between the number density of the inhibiting species at time of transfer and the number of specimens present in the chamber at the end of the experiment.

Airborne allomonal interactions were similarly examined. Spearman's rank order correlations were run between both final culture number densities and maximum culture number densities and for average culture densities for each interacting species pair. The only inverse correlations found were between *F. candida* and *X. grisea*. Here there was a significant (P = .04 and .05) negative correlation between terminal population size in both species. In all other combinations the correlations were nil (generally P > .50).

4. Comparison with earlier studies

4.1. Number density dependence

Our findings agree with VERHOEF's conclusion that pheromone production in *Tomocerus minor* (LUBBOCK) and *Orchesella cincta* (LINNAEUS) diminishes with increasing population density (VERHOEF, 1984). They might conflict with the results of LONGSTAFF (1976) who found that the outcome of direct interaction experiments can usually be strongly affected by initial numbers of individuals.

4.2. Direct interaction

Table 3 summarizes results of direct interaction studies so far carried out. *F. candida* and *S. curviseta* both appear to generally dominate in interspecific interactions. This is hardly surprising since both species are very common in greenhouses, and indoor flowerpots, the kind of controlled conditions represented in the culture containers. A more surprising consistent winner was *P. schoetti* which has restricted ranges and is normally found in wet habitats (VAN COTT, 1982 unp. thesis). The small number of replicates (2 or 3) involved in his work makes conclusions concerning these results tentative. It is notable that viewing all workers' results 76% of the interactions were of type 1, with 12% type 2, and 12% type 3. It is also striking that while only half of the type 2 or 3 interactions were consistent (i.e. were always the same under different experimental conditions and in all replicates), 73% of the type 1 interactions were consistent.

Table 1. Reported examples of collembolan allomones and pheromones.

Species	Effect	Reference
Folsomia candida	P, aggregation;	LEONARD & BRADBURY, 1984
Folsomia candida	P, A, Population growth;	*
Sinella curviseta	P, sexual;	WALDORF, 1974
Sinella curviseta	P, A, population growth;	VAN COTT, 1982
S. caeca	P, A, Population growth;	*
Pseudosinella violenta	P, A, population growth;	*
Heteromurus nitidus	P, aggregation;	KROOL & BAUER, 1987
Orchesella cincta	P, aggregation, activity;	VERHOEF *et al.*, 1977
	P, reproduction;	MERTENS *et al.*, 1979, VERHOEF & MERTENS, 1984
O. villosa	P, aggregation;	VERHOEF *et al.*, 1977
Tomocerus minor	P, aggregation, activity, reproduction;	MERTENS, 1984
Onychiurus armatus	P, aggregation;	JOOSSE & KOELMAN, 1984
Xenylla grisea	P, A, population growth;	*
Hypogastrura viatica	P, aggregation;	MERTENS & BURGOIGNE, 1977
H. lapponica	P, developmental; synchronization;	LEINAAS, 1983

A = allomone, P = pheromone * — in this work

4.3. Substrate conditioning

VAN COTT (1982 unpublished thesis) established that substrate conditioning by *Cryptopygus thermophilus* and *Entomobrya guthriei* inhibited the population growth of *C. thermophilus* when compared to growth in new culture dishes. He also established that the same thing happened with the above species and *Proisotoma schoetti* in chambers conditioned by *S. curviseta*. He tested self inhibition only in *S. curviseta*. He found that this species had a stronger inhibition of itself than it does of the other species. In contrast, our studies showed no clear evidence of self inhibition by substrate conditioning. We established that interspecific substrate conditioning inhibited population growth more than conspecific substrate conditioning in almost all cases studied. The two exceptions were that *X. grisea* did not inhibit growth in *F. candida* and *P. violenta* inhibited growth in *F. candida* only briefly.

4.4. Pheromones and allomones in Collembola

It might be argued that the results of the airborne chemical experiments did not necessarily involve pheromones and allomones. WALDORF (1971) has shown that volatile substances produced in cultures of *Sinella curviseta* have the capacity to inhibit oviposition. She suggested that these substances were probably the products of the food yeast metabolism; however, the variety and high specificity of results, in our view, argues in favor of this being caused by pheromones and allomones.

The most consistent result in the airborne experiments was the negative pheromonal effect (3 out of 4 cases). While the results were statistically significant in only one case, the others strongly suggest a negative effect (figs. 2E, 3A & 3E). *P. violenta* shows no allomonal effects while the other three species do, but these can be either inhibitory or stimulatory. Stimulatory effects tend to be temporary and the populations peak early (6–8 weeks) while inhibitory effects occur later and persist.

While a number of explanations for the substrate conditioning effects are possible, again the high specificity of interaction suggests that the secretion of pheromones and allomones

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Table 2. Different regulatory effects.

Affected species	Affecting species	Direct interaction	Substrate conditioning	Airborne chemicals
F. candida	*S. caeca*	−?	−	+?
F. candida	*X. grisea*	+ temporary	0	+
F. candida	*P. violenta*	0	− temporary	0
F. candida	*F. candida*	?	0	0
S. caeca	*F. candida*	−	−	−
S. caeca	*X. grisea*	0	−	0
S. caeca	*S. caeca*	?	0	−?
X. grisea	*S. caeca*	−	−	−
X. grisea	*F. candida*	−	−	+
X. grisea	*X. grisea*	?	0	−
P. violenta	*F. candida*	−	−	+
P. violenta	*P. violenta*	?	−	+?

symbols: − = decrease pop. growth, 0 = no effect, + = increase population growth. ? after symbol indicates apparent but not statistically significant effect.

is the most probable one. Water borne chemicals can act as pheromones (MERTENS & BOURGOIGNE, 1977; MERTENS *et al.*, 1979). VERHOEF (1984) established that faeces contained pheromones but that pheromones had to be also transmitted by other means. Since most of VAN COTT and all of our experiments involved the removal of fecal pellets and exuviae, other transmittal mechanisms are likely. Table 1 summarizes our present information concerning collembolan pheromones and allomones. WALDORF (1974), VERHOEF *et al.* (1977), LEONARD & BRADBURY (1984) & LEINAAS (1983) have presented evidence that some collembolan pheromones can be airborne.

The discovery that airborne pheromones and allomones can affect population growth in Collembola adds to our rapidly increasing understanding of the importance of these in collembolan biology. The evidence that allomones can influence population growth suggests that they may be a major factor in determining Collembola community makeup.

5. Discussion

While it is clear that environmental conditions can sometimes affect the outcome of laboratory interaction studies with Collembola (CHRISTIANSEN, 1967; CULVER, 1975; LONGSTAFF, 1976), those tested so far did not do so in most cases (CHRISTIANSEN, 1967; CULVER, 1975; LONGSTAFF, 1976; and VAN COTT, 1982). It is also clear that results can be highly variable, although some species were generally dominant in interspecific interactions (See table 3).

Many mechanisms have been suggested for interspecific interactions in Collembola (CHRISTIANSEN, 1964; JOOSSE & VERHOEF, 1974; LEINAAS, 1983; LEONARD & BRADBURY, 1984; LONGSTAFF, 1976; MERTENENS *et al.*, 1979; VERHOEF & NAGELKERTE, 1977; VERHOEF, 1984; WALDORF, 1971, 1975) and our present studies would indicate that there were, in most if not all cases, several mechanisms at work at once. Table 2 summarizes the results of our present study. It should be noted that in some cases the results of all 3 sets of experiments were the same. Thus *F. candida* had a uniformly negative effect on *S. caeca* and the latter in turn had a uniformly negative effect on *X. grisea*. In all other cases the effects were different from one treatment to another. The direct interaction experiments would clearly involve both substrate conditioning and airborne factors. In the two cases above the resultant population growth inhibition in direct interaction might simply result from a combination of these two factors; however, direct contact would also allow

Table 3. Summary of results of direct interaction studies.

	I_n	F_c	S_{cu}	S_{ca}	T_m	X_g	H_m	H_d	A_d	A_c	S_q	P_v	P_{sc}	P_{se}	C_t	E_g	L_c	O_a
I. notabilis	X	1B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
F. candida	A	X	2B	2D 1B	1B	1B	2	1B	–	–	–	1B	–	–	–	–	1B 3	–
S. curviseta	–	A	X	3	1C	1C	–	–	–	–	–	–	1C	1C	1C	1C 3?	–	–
S. caeca	–	A, C	A	X	–	3?	–	1D 3*	–	–	–	–	–	–	–	–	–	1D
T. minor	–	A	A	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–
X. grisea		A, C	A	C	–	X	–	–	–	–	–	–	–	–	–	–	–	–
H. manubrialis	–	A	–	–	–	–	X	–	1J or G	1J or G	–	–	–	–	–	–	–	–
H. (C.) denticulata	–	A	–	E	–	–	–	X	–	–	–	–	–	–	–	–	–	1R or H*
A. dubius	–	–	–	–	–	–	A	–	X	–	–	–	–	–	–	–	–	–
A. caecus	–	–	–	–	–	–	A	–	–	X	2 1	–	–	–	–	–	–	–
S. quadrimaculata	–	–	–	–	–	–	–	–	–	A	X	–	–	–	–	–	–	–
Ps. violenta	–	C	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–
Pr. (B.) schoetti	–	–	B	–	–	–	–	–	–	–	–	–	X	1M	1M	1M	–	–
Ps. sexoculata	–	–	B	–	–	–	–	–	–	–	–	–	B	X	1N	1N	1Q	–
C. thermophilus	–	–	B	–	–	–	–	–	–	–	–	–	B	B	X	1P	–	–
E. (E.) guthriei	–	–	B	–	–	–	–	–	–	–	–	–	B	B	B	X	–	–
L. cinereus	–	D	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–
O. (P.) armatus	–	–	–	E	–	–	E	–	–	–	–	–	–	–	–	–	–	X

Below = reference
A – Christiansen '67
B – Van Cott '82
C – Present work
D – Culver '74
E – Longstaff – '76

Above = interaction
1) = 1 species eliminating others (dominates from start)
2) = 1 species dominates at first with second taking over at end
3) = coexistence or no clear dominance

Letter = dominating species
* outcome changed by differing environmental conditions.

other mechanisms to operate. Oophagy, sperm packet destruction and aggressive interactions over food have all been shown to occur in Collembola. These could only occur in direct interaction and should have a negative effect upon reproductive success. To support the idea of additional factors coming into play when direct interaction obtains we note that when there was a negative effect in both direct interaction and other factors the effect was generally much more striking in direct interaction than in substrate conditioning or airborne factors. Compare the effects of F. candida seen in fig. 2A with that in 2D or 3C and 3D & 3F. It was striking that there is no consistency among species interactions in the way the different types of interaction vary. Thus while *S. caeca* had a negative effect upon population growth in *F. candida* in direct interaction and substrate conditioning, it appears to have had a positive effect in airborne contact. The effect of *F. candida* upon *X. grisea* and *P. violenta* appears to be similar. In contrast *P. violenta* had a strong negative effect upon *F. candida* in substrate conditioning tests but no effect otherwise.

It is also striking that the pheromonal effects seen in this study (examined separately only in the airborne experiments) were preponderantly negative (75%) while the airborne allomonal interactions are predominantly neutral or positive (75%). **This would suggest that there were different mechanisms at work in substrate mediated interaction, airborne chemical mediated interaction and at least sometimes in direct interaction.**

Given the nature of normal habitats for these species, in small enclosed spaces with relatively little animal mobility, it is probable that under different circumstances direct interaction, substrate conditioning or airborne factors could most important in interspecific interaction. Since these can have opposing effects this could be well explain the conflicting nature of many reports of interspecific interaction. If this or a similar array of mechanisms is available in other animals, it would present a very different view of the nature of interspecific interaction from that usually taken.

The inhibition of population growth by substrate conditioning appears to be insensitive to the density of the animals of the inhibiting species.

As with the substrate conditioning studies, the airborne allomonal effects were not generally clearly dependent upon the density of the affecting species.

How then could the interactions of our present studies be categorized? We have been unable to apply any of the definitions of competition cited by KEDDY (1989) to any of the interactions we have studied. We have the problem that, in many cases, interactions could be amensal, competitive, or commensal, depending upon which kind of mechanism was dominant in the particular interaction between the species.

While it is possible that the kind of complex interaction we have seen is a very unusual phenomenon, this possibility has not been tested anywhere else to our knowledge.

6. Conclusions

J. N. THOMPSON (1988) has shown how interspecific interactions vary strikingly under a variety of differing population structure and environmental conditions. We studied interactions among four ecologically similar species of Collembola under three different sets of laboratory conditions. We found that the interactions involved 3 different mechanisms which often had differing outcomes. They varied from inhibitory to stimulatory. Since, given the nature of collembolan habitats, each of these mechanisms is most important under different circumstances, the interspecific interaction between populations can vary from negative to nil to positive under different sets of conditions. Thus it is difficult to identify the relationship between the species as being competitive, amensal, etc. without clear knowledge of the exact fashion in which the species interact under the circumstances being studied.

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